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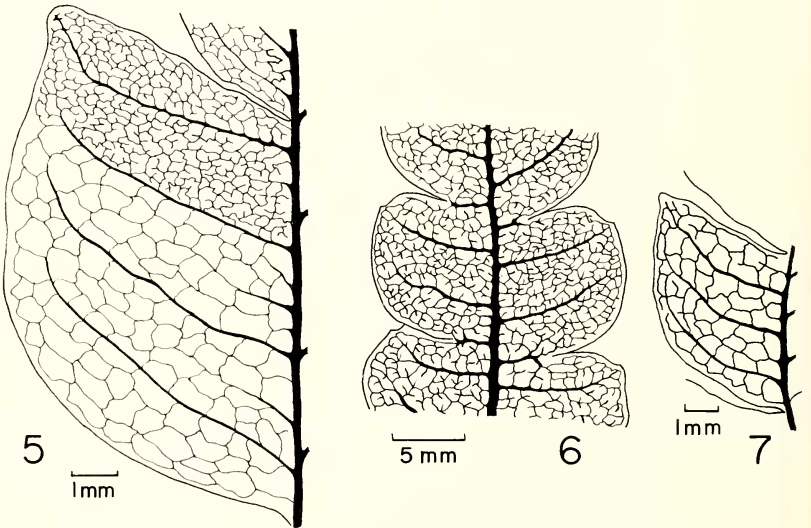
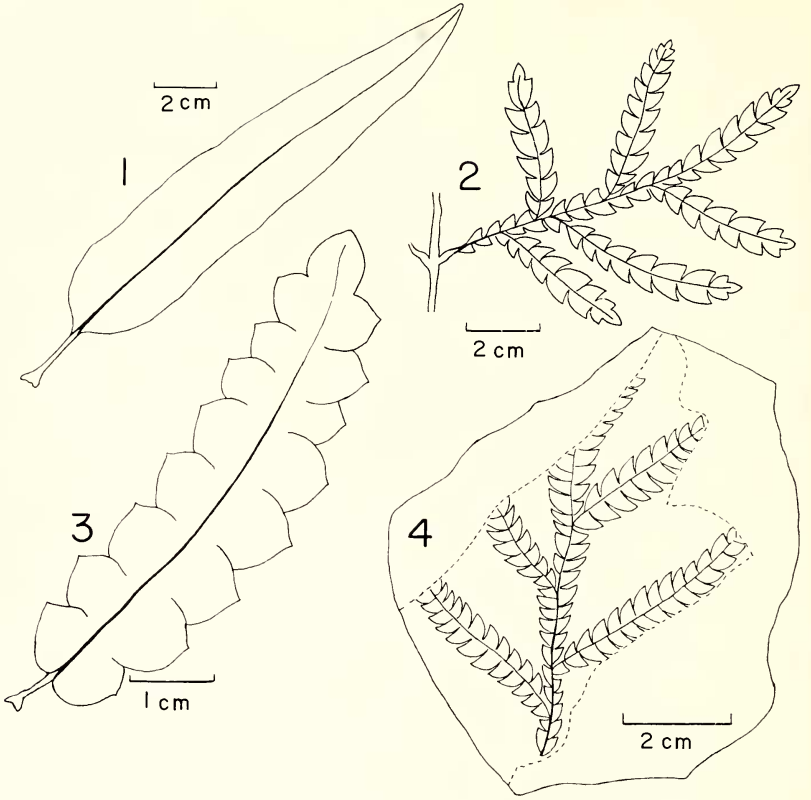
FOSSIL LEAVES OF LYONOTHAMNUS

SATISH C. BANWAR

Leaves of the extant genera *Lyonothamnus*, belonging to the family Rosaceae, and *Comptonia*, belonging to the family Myricaceae, are very similar in external appearance. Many paleobotanists who have examined fossil leaves of *Lyonothamnus* were at times led to identify them as *Comptonia*. This study was conducted to examine and compare leaves of *Lyonothamnus*, both extinct and extant, and those of *Comptonia*, so that differences and similarities in shape, nature, and venation could be established, which would then help to distinguish them.

Fossil leaves, identified as those of *Lyonothamnus*, have been collected in various localities in the western United States from Washington to Oregon, California, and Nevada. The ages of all these fossil leaves range from Miocene to Pliocene. All the specimens collected so far are comparable to leaves of the extant *L. floribundus* Gray ssp. *asplenifolius* (Greene) Raven. The leaves of subspecies *asplenifolius* are so distinctive that similarities with the fossil forms are easily recognized (figs. 2, 4). So far, to my knowledge, no one has reported the presence of fossil leaves which may be comparable to foliage of subspecies *floribundus* (fig. 1).

The first fossil specimens to be identified as *Lyonothamnus* were collected by Axelrod in 1939 from the Tehachapi area of California; he



described and named these specimens as *L. mohavensis* (Axelrod, 1939). The age of these specimens was determined as Middle Miocene; they were in small fragments and only portions of leaflets were present, but the general appearance, shape, and venation were similar to those of leaves of living *L. floribundus* ssp. *asplenifolius*. Since then Axelrod has reported the occurrence of *L. mohavensis* from many other localities in California and Nevada. The sites and their ages are as follows: Furnace Creek Flora, California (Mio-pliocene), Mint Canyon Flora, California (Upper Miocene), Upper Modella Flora, California (Upper Miocene), Coal Valley Flora, Nevada (Upper Miocene), Mulholland Flora, California (Middle Pliocene) (Axelrod, 1940). In 1956, while examining the Mio-pliocene floras from west-central Nevada, the same author described many fossil specimens as *C. parvifolia*, because to him they resembled the leaves of members of the extant genus *Comptonia* (Axelrod, 1958). These leaf specimens reported as *Comptonia* were much larger and better preserved than those reported earlier as *Lyonothamnus*.

Wolfe, while investigating the Miocene floras from Fingerrock Wash, Nevada, reassigned *C. parvifolia* to *L. parvifolia* (Axelrod) Wolfe. He justified his reassignment on the basis of venation pattern (Wolfe, 1964). Wolfe also believed he could distinguish two forms of fossil *Lyonothamnus*: one form having seven to nine leaflets or pinnae and the other fewer than seven leaflets. The former represents *L. parvifolia*, the latter *L. mohavensis*. He was of the opinion that these two forms should be regarded as two different species, and that *L. mohavensis* is closer to the extant forms.

Page (1964) has recently described as *Lyonothamnoxylon nevadensis*, fossil wood from the lower Pliocene of Nevada. The wood of *L. nevadensis* most closely resembles that of *Lyonothamnus*.

The genus *Lyonothamnus* comprises a single living species with two subspecies (Raven, 1963), namely *L. floribundus* Gray ssp. *floribundus* and *L. floribundus* ssp. *asplenifolius* (Greene) Raven. The genus is endemic to the islands off the shores of southern California; no natural population exists on the mainland. The distribution of the subspecies on the islands is also very interesting. Subspecies *floribundus* is confined to Santa Catalina I., while ssp. *asplenifolius* is restricted to Santa Rosa, Santa Cruz, and San Clemente islands. The two subspecies are distinguished from each other by the nature and form of the leaves they bear. The leaves of ssp. *floribundus* are simple, lanceolate, and have an entire margin (fig. 1), while those of ssp. *asplenifolius* are pinnately compound

FIGS. 1-7. *Lyonothamnus* and *Comptonia*: 1, leaf of *L. floribundus* ssp. *floribundus*; 2, leaf of *L. floribundus* ssp. *asplenifolius*; 3, leaf of *C. peregrina* showing the lobes (Transylvania Co., North Carolina, Fox 704, UC); 4 fossil specimen of *L. parvifolia*, collected by the author at Stewart Springs area, Mineral Co., Nevada; 5, a leaf lobe of *L. floribundus* ssp. *asplenifolius*, showing venation pattern; 6, portion of leaf *C. peregrina*, showing venation of lobes; and 7, a leaf lobe of *L. parvifolia*, showing venation pattern.

and have a dissected lamina (fig. 2).

The members of the genus *Comptonia* are confined in their distribution to the eastern United States. The leaves of *C. peregrina* (L.) Coult. (fig. 3) are simple, and the laminae are dissected somewhat like those of *L. floribundus* ssp. *asplenifolius*.

MATERIALS AND METHODS

Fossil specimens were examined in the excellent collections of the Museum of Paleontology, University of California, Berkeley. Some specimens were collected personally from Stewart Springs, Mineral Co., Nevada. They [fossil leaves] were examined under a dissecting microscope, and the venation patterns were observed by wetting the specimens with clove oil.

Leaves of living plants of *Lyonothamnus* were obtained from the Rancho Santa Ana Botanical Gardens at Claremont and from the University of California Campus at Berkeley. At both of these places the trees are cultivated. Leaves of *C. peregrina* were obtained from herbarium specimens housed in the University of California Herbarium, Berkeley.

The leaves of *Lyonothamnus* and *Comptonia* were found to be very rich in tannin and thus the clearing technique had to be modified slightly. Both dried and fresh leaves were boiled in water and then in alcohol to remove the chloroplasts. The leaves were then washed in running tap water for some time and soaked in My-pro Bleach (manufactured by Crown Products, San Francisco), which removed all the tannin and made the leaves white. The timing in this bleach had to be adjusted for each leaf because a prolonged treatment in bleach macerated all the tissues. After this the leaves were washed again in tap water for several hours and then soaked in a saturated solution of chloral hydrate. They were then washed in water and stained in the usual way with 1 percent alcoholic safranin. It was found that dried plant materials yielded better results than did similarly treated living materials. The leaves were mounted in Picolyte on large glass plates.

OBSERVATIONS

Most of the fossil specimens examined are only fragments of large leaves. Some of these fragments are fairly large while others are small, but even from the latter it was evident that the original laminae were pinnately compound and that each pinna had several dissected lobes. The definite number of pinnae present on each leaf could not be determined because of the small size of the fragments or their arrangement. Some of them have as few as three pinnae, while others have as many as nine. The lobes are not exactly opposite each other on a pinna but are "staggered" or arranged alternately. Each lobe is somewhat triangular in shape with an acute pointed apex. The lobes are sessile and attached by one complete side to the axis of the pinna (fig. 4).

In each lobe, several secondary veins are given off from the axis of the pinna. These extend nearly to the margin of the lobe. Each secondary vein produces several tertiary veins, which also divide further and form a fine network of veins. The finer details and the details of the vein endings could not be examined as they were not well preserved in the fossils. Among the secondary veins, it is the uppermost (or first) secondary vein which terminates in the apex of the lobe, while the other secondary veins form a loop at the distal margin and join with the secondary vein above (fig. 7).

In the genus *Lyonothamnus*, only leaves of ssp. *asplenifolius* were examined in detail because it is in this subspecies that similarities have been noted with the various fossil leaves mentioned and with leaves of *Comptonia*.

Leaves of *L. floribundus* ssp. *asplenifolius* are opposite (although members of the Rosaceae are usually considered to have alternate leaves) and pinnately compound with several pinnae (fig. 2). The number of pinnae varies between three and seven on different trees and even on different branches of the same tree. No leaf was observed to have as many as nine pinnae. Each pinna is divided into several lobes, the sinuses extending clear into the axis of the pinna. These are slightly staggered or alternate to each other on the axis of the pinna, and are sessile and triangular in outline. Each lobe has an acute apex and one complete side is attached to the axis of the pinna (fig. 2). In each lobe, several secondary veins are given off from the axis of the pinna and extend nearly to the margin of the lobe. Each secondary vein produces several branches which divide further and produce a fine network of veins with free vein endings. It is the uppermost (first) secondary vein which terminates in the apex of each lobe (fig. 5), while the other secondary veins form loops near the distal margin and join with the adjacent secondary vein towards the apex.

Leaves of *C. peregrina* are alternate and simple. The lamina is dissected into nearly opposite lobes, but the sinuses do not extend all the way to the midrib (figs. 3, 6). The size of the leaves varies and so also does the number of the lobes. But it is evident that the lobes are very different from those of *Lyonothamnus*. Each lobe has an obtuse apex. Generally three secondary veins develop in each lobe, the first extending only to the sinus, and (in contrast to the situation in *Lyonothamnus*) the second or central secondary vein terminating in the apex of the lobe (fig. 6). Each secondary vein produces several tertiary veins which divide further and produce a fine network of veins with free vein endings.

DISCUSSION

From the external morphology of the leaves studied, it is very clear that the fossil leaves of *Lyonothamnus* are very similar to those of the extant ssp. *asplenifolius*. The similarity with leaves of *Comptonia* is

very superficial. The leaves of *Comptonia* are simple, the incisions of the lamina are shallow, and the lobes are opposite or nearly so, while those of *Lyonothamnus* are compound with a number of pinnae and the incisions of the lamina are deep, extending right up to the axis of the pinna. The shape, position, and nature of the lobes and their apices are also very different.

The venation patterns are also distinct. The venation of both extant and fossil leaves of *Lyonothamnus* examined were very similar. In both it is the first, or uppermost, secondary vein which terminates in the apex of the lobe. In *Comptonia* it is the second, or the central, secondary vein which does so. Thus on the basis of venation pattern also the fossil leaves show a greater similarity with those of the extant ssp. *asplenifolius*. The similarity with those of *Comptonia* is very superficial.

This study agrees with the views of Wolfe in reassigning all the fossil leaves described as *C. parvifolia* Axelrod to *Lyonothamnus parvifolia* (Axelrod) Wolfe, although the creation of two species among the fossil leaves is debatable.

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Hearngunje, Hazaribagh, Bihar, India

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NOTES AND NEWS

EDITORSHIP OF MADROÑO.—Some time during the summer of 1971, Dr. Robert Ornduff, Department of Botany, University of California, Berkeley, will become the Editor of Madroño. At the same time, Dr. John Strother, also at Berkeley, will become Managing Editor. In preparation for the change of Editors, it is requested that all new manuscripts intended for publication in Madroño be sent to Berkeley rather than Stanford.